PREY SELECTION BY TIGERS *PANTHERA TIGRIS* (LINNAEUS 1758) IN THE SUNDARBANS EAST WILDLIFE SANCTUARY OF BANGLADESH

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This study was conducted to determine prey selection by Tigers *Panthera tigris* in the Sundarbans East Wildlife Sanctuary of Bangladesh. A total of 145 scats were analysed and 78 kills were studied. The frequency of occurrence of different prey species in scats and kills was significantly different. On an average, the Spotted Deer *Axis axis* was the most frequent prey in scats and kills (78%). Most Spotted Deer kills were adult animals and were in good condition before they were killed. The frequency of occurrence in scats was converted to the relative number of kills, which showed that the Spotted Deer was still the most frequent prey (29.9%). Other than the Spotted Deer, tigers also preyed on Wild Boar *Sus scrofa*, Rhesus Macaque *Macaca mulatta*, and Lesser Adjutant *Leptoptilos javanicus*. Soil and sungrass blades were found in scats as non-food items. Scats with soil were more available in winter than in summer. In general, the trend of prey selection appeared to follow prey size and abundance, but Wild Boar and Lesser Adjutant were two most high-ranking prey species, because their selectivity was higher in comparison to their abundance.

Key words: mangroves, tiger food habit, tiger kills, tiger scats, spotted deer

INTRODUCTION

The acquisition of food is a fundamental component of every predator's daily existence. Hence, knowledge of food selection is critical to understanding life history strategies and developing sound conservation recommendations (Miquelle *et al.* 1996). Predatory strategies are shaped and refined by natural selection to maximise nutrient intake within the bounds of a wide range of biologically relevant ecological constraints (Clutton-Brock and Harvey 1983; Sunquist and Sunquist 1989). Carnivores often regulate or limit the numbers of their prey, thereby altering the structure and function of entire ecosystems (Schaller 1972; Smuts 1978; Berger *et al.* 2001; Terborgh *et al.* 2002). The role Tigers *Panthera tigris* play as top predators is vital to regulating and perpetuating ecological processes and systems (Sunquist *et al.* 1999; Terborgh 1999). The analysis of food habits provides practical and immediately useful information for the management of a particular species, and occasionally aids law enforcement and management needs (Korschgen 1971).

The general objective in this research is to identify whether Tigers in the Sundarbans have any preference for prey in terms of species, availability, age and health. The specific questions are: 1) What are the proportions of different prey species in Tiger scats and kills? 2) Do Tigers sometimes ingest non-food items? 3) Does prey abundance have any effect on prey selection? 4) What are the proportions of kills in different age and health classes? 5) Does the abundance of the Spotted Deer *Axis axis* in different age classes have any effect on its selection?

MATERIAL AND METHODS

Study area

The study was conducted in a part of the Sundarbans. The entire Sundarbans is an area of about 10,000 sq. km in the Ganges-Brahmaputra delta of Bangladesh and India, but roughly 60% of this forest lies in the south-west of Bangladesh and the rest 40% is in the south-east of the Indian state of West Bengal. The monthly mean temperature and relative humidity normally varies from 23 °C (during December-January) to 35 °C (during May-June) and from 70% to 80%, respectively. There are three wildlife sanctuaries in the Bangladesh Sundarbans that together form a UNESCO World Heritage Site. The Sundarbans East Wildlife Sanctuary (WS) (312 sq. km) is one of these three sanctuaries where this research was concentrated (Fig. 1). Geographically the area is located between 21° 47'-22° 03' N and 89° 44'-89° 56' E.

Scat analysis

The scat samples were collected from the field, on a monthly basis, for 18 months (September 2001 to February 2003). Since the Tiger is the only large carnivore in the Sundarbans, Tiger scats could be identified without any confusion. The samples were sun-dried whenever necessary, preserved in a tagged polythene bag, and brought to the laboratory for analysis. At first, each of the dried scats was classified according to the relative volume, weighed using the Lark JPT-2 (range: 0.1-200 gm) beam balance (big scats were weighed in sections), and were classified according to their weight. Then each scat was broken and carefully soaked in water to separate prey remains, such as hair, bones, hooves, teeth,

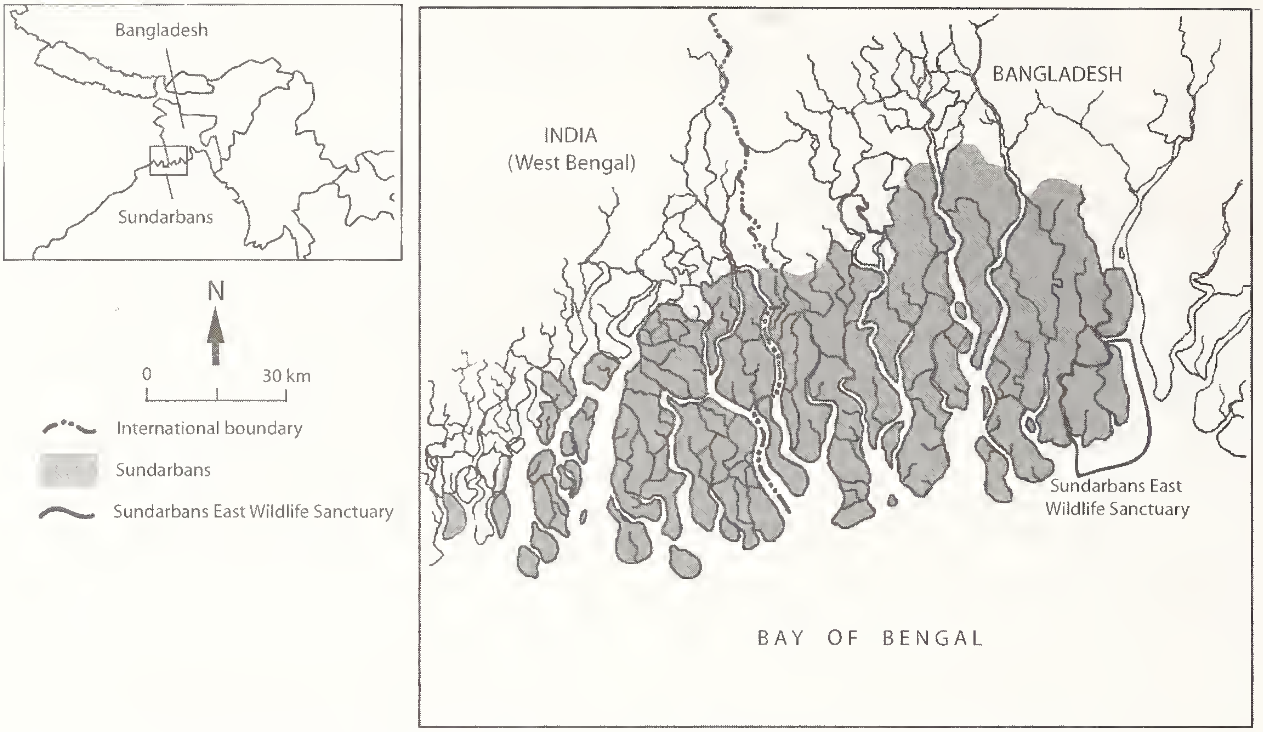

Fig. 1: The Sundarbans of Bangladesh and India showing the Sundarbans East Wildlife Sanctuary

feathers. The separated items were studied with the unaided eye and with a magnifying glass, as well as under a light microscope, if necessary, and were identified by comparing with a reference collection (from different species of kills and from captive animals) using features such as structure, colour, and medullary configuration to identify prey species (Koppikar and Sabnis 1976; Amerasinghe 1983; Kitsos *et al.* 1995; Ramakrishnan *et al.* 1999). The remains of one prey species in one scat were considered as frequency one. If there were remains of two prey species in a scat (which was a rare case; found only in a few scats), the frequency was divided into 0.5 for each prey species. The non-food items were recorded when the item formed more than 50% of the scat volume (Schaller 1967; Johnsingh 1983), but these were excluded while estimating diet composition and the biomass of food consumed (Reynolds and Aebischer 1991). Reynolds and Aebischer (1991) defined non-food items in the scats as remains of ingesta that have little or no nutritive benefit (i.e., soil and sungrass in this study).

To determine whether the scat sample size is sufficient, the method was followed from Mukherjee *et al.* (1994), who studied the effect of scat sample size on frequency of occurrence in scats of a given prey species and identified the minimum reliable sample size (MRSS) as that which does not cause any further change in a prey with increase in sample size.

Although the frequency of occurrence of prey species in carnivore scats is a commonly-used parameter in the study of carnivore food habits, if prey size is highly variable (as in this study), the frequency of occurrence can considerably distort the relative numbers of different prey species in the diet (Panwar 1990; Karanth and Sunquist 1995). However, the frequency of occurrence of different prey species in the scats of Tigers can be converted to relative numbers and biomass of different prey taken, which represents the actual selectivity pattern (Floyd *et al.* 1978; Ackerman *et al.* 1984; Karanth and Sunquist 1995). In the light of the previous approaches (Schaller 1967; Johnsingh 1983; Putman 1984; Emmons 1987; Karanth and Sunquist 1995), the method developed by Ackerman *et al.* (1984) for Puma *Puma concolor*, to convert the frequencies of occurrence into relative numbers and biomass of individuals killed, was used. Assuming that the digestive system and the degree of carcass use of the Tiger is comparable to that of the Puma, the following regression was used to relate live weight of prey killed (X) to the weight of that prey represented in one field-collectable Tiger scat (Y) –

$$Y = 1.980 + 0.035\ X$$

The average number of collectable scats produced by a Tiger from an individual animal of each prey species ($\lambda_i = X/Y$), and the relative numbers of each prey killed were computed from the above equations (Ackerman *et al.* 1984). The relative numbers were then converted to relative biomass by multiplying with the minimum adult weight.

Prey selectivity index

The selectivity index (S) (Sourd 1983; Julliot 1996), used to compare the abundance of each edible prey species in the habitat and its proportion in the Tiger diet, was calculated by using the equation mentioned below –

$$S = (PC_{sp} - PA_{sp})/(PC_{sp} + PA_{sp})$$

Here PC_{sp} = proportion of one particular prey species in the Tiger diet as a percentage of the relative number of that prey species in the Tiger diet (Spotted Deer *Axis axis* = 43.4, Wild Boar *Sus scrofa* = 8.5, Rhesus Macaque *Macaca mulatta* = 22.2, Lesser Adjutant *Leptoptilos javanicus* = 8.5, Red Junglefowl *Gallus gallus* = 17.4, Water Monitor *Varanus salvator* = 0; Table 3), and

PA_{sp} = proportion of the same prey species available in the habitat as a percentage of the individual density of that prey species in total prey population (Spotted Deer = 48.2, Wild Boar = 1.1, Rhesus Macaque = 15.0, Lesser Adjutant = 1.4, Red Junglefowl = 16.1, Water Monitor = 18.2; Khan 2004).

The species was then considered as: a) a high-ranking species, when $S > 0.3$ (PC_{sp} at least double than PA_{sp}); b) a middle-ranking species, when S lies between -0.3 and 0.3 (PC_{sp} similar to PA_{sp}); c) a low-ranking species, when $S < -0.3$ (PC_{sp} at least half than PA_{sp}); and d) an uneaten species, when $S = -1$ ($PC_{sp} = 0$, non-used edible species).

Kill study

Crows and vultures are good advertisers of Tiger kills in most of the Tiger ranges of the Indian subcontinent (Schaller 1972; Johnsingh 1983; Karanth and Sunquist 1995), but the dense vegetation, and the rarity of crows and vultures in the Sundarbans, forced me to depend mainly on odour and dragging signs. In addition to the species of prey killed, if the kill was relatively intact, the age class and health of the killed individual was recorded on the basis of the size, colour and overall condition of the animal. Whenever possible, the colour and texture of femur marrow fat were examined in order to record the health condition of the kill more accurately (Schaller 1967; Sinclair and Duncan 1972; Riney 1982). The lower jaws were collected whenever available, and taken to the laboratory where the total length and diastema length were measured, and used to classify the kills into age categories as adult, yearling/juvenile and fawn/young on the basis of eruption and wear of premolar and molar teeth (Schaller 1967; Riney 1982; van Lavieren 1983). I also tried to determine the age of kills by counting tooth cement rings (Ashby and Santiapillai 1986; Ballard *et al.* 1995; Landon *et al.* 1998), but no distinct annuli were found.

Selectivity of the Tiger predation for age classes of the Spotted Deer was assessed by Ivlev's selectivity index (D) (Okarma *et al.* 1997; Khorozyan and Malkhasyan 2002) –

$$D = (fE - fL)/(fE + fL - 2fEfL)$$

Here fE = fraction of a given age class among Spotted Deer eaten by Tigers (adult = 0.765, yearling = 0.176 and fawn = 0.059; ages identified on the basis of the eruption of the teeth (Table 5), and fL is the fraction of a given age class in the habitat (adult = 0.722, yearling = 0.205 and fawn = 0.073; Khan 2004). The positive or negative value of D for a certain age class means that the individuals of that age class were positively or negatively selected.

RESULTS

Scat volume and weight, and minimum sample size

In terms of relative volume, there were no significant difference in the frequencies of small, medium and large scats ($\chi^2 = 0.68$, df = 2, $p = 0.713$), but medium-sized scats were the commonest (36.6%). On the other hand, classes based on dry weight show that there were significant differences in the frequencies of scats in three different weight classes ($\chi^2 = 25.00$, df = 2, $p < 0.001$), but relatively light weight (<100 gm) scats were the commonest (51.0%) (Table 1). The mean weight of dried scats was 124.9 gm (n = 145, range = 10.6-406.6 gm, sd = 94.8).

The results of the test for minimum sample size of the scats, required for actual presentation of the proportion of a prey species in the scats is illustrated in Fig. 2. It is evident that even 34 samples are sufficient to represent adequately the occurrence of the Spotted Deer in the Tiger diet, which stays virtually steady-state regardless of the larger sample size.

Prey selection

The frequency of occurrence of different prey species in scats and kills (Table 2) shows that excluding zero values, the frequencies of different prey species were significantly different (in scats: $\chi^2 = 545.71$, df = 7, $p < 0.001$; in kills: $\chi^2 = 316.15$, df = 6, $p < 0.001$). On an average, Spotted Deer

Table 1: Scat size of the Tiger on the basis of volume and weight

Relative volume			Weight (gm)		
Class	No.	%	Class	No.	%
Small	46	31.7	<100	74	51.0
Medium	53	36.6	100+ to 200	46	31.7
Large	46	31.7	200+	25	17.3

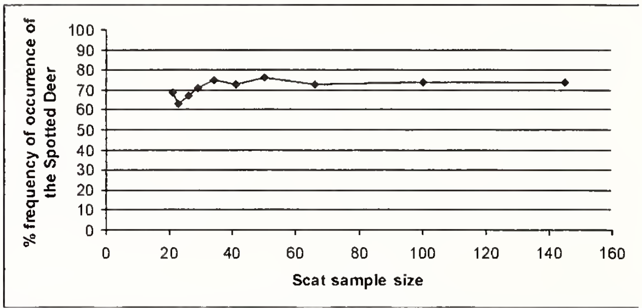

Fig. 2: Relationship between the sample size of Tiger scats and percentage of the frequency of occurrence of the Spotted Deer in scats in the Sundarbans East Wildlife Sanctuary

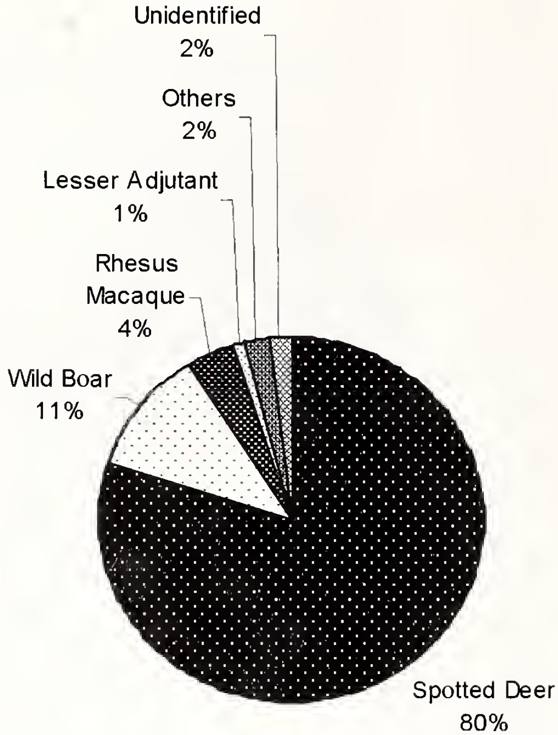

Fig. 3: Proportions of the relative biomass of different prey species consumed by Tigers in the Sundarbans East Wildlife Sanctuary

was the most frequent (78%), but Tigers also consumed Wild Boar, Rhesus Macaque, Porcupine (Indian Crested *Hystrix indica* or Brush-tailed *Atherurus macrourus*), Leopard Cat *Prionailurus bengalensis*, Irrawaddy Dolphin *Orcaella brevirostris* (died in the fishing net, which was thrown away and floated to the bank, and finally eaten by the tiger), Lesser Adjutant, Red Junglefowl, Mud Crab *Scylla serrata* and Water Monitor *Varanus salvator*, which together form the rest of the frequency percentage (Table 2). Since the prey sizes varied considerably, the frequency of occurrence was converted to the relative numbers of prey animals killed, and it was found that Spotted Deer was still the most frequently consumed (29.9%) (Table 3). When relative numbers of different prey animals consumed by Tigers were converted to the relative biomass, it shows that the Spotted Deer forms the bulk of the diet (80%) and Wild Boar is the second-most consumed (11%) (Fig. 3). These are the two species on which Tigers in the Sundarbans are thriving.

Non-food items in scats

Other than the prey animal remains, 74 (51%) scat samples had large quantities of soil (more than 50% of the volume). Sungrass (*Imperata* sp.) blades, and rarely leaves, were also found in a number of scats, but only one scat (collected in January 2002) had sungrass more than 50% of the volume. In almost all cases the soil was very hard in the scat, probably due to contraction in the intestine. The occurrence of scat samples with more than 50% soil in different periods of the months was significantly different ($\chi^2 = 27.19$, df = 8, $p = 0.001$). More than 80% of the scats with soil were found in winter/dry season (October-March), with the peak in November-December (*c.* 15%), which indicates a strong seasonality in soil ingestion by Tigers (Fig. 4). Notably, the monthly total collection of scats was almost equally proportional in different seasons. The presence

Table 2: Occurrence of different prey species in scats and kills of Tigers

Prey species	Frequency in scats	% frequency in scats	Frequency in kills	% frequency in kills	% total frequency in scats and kills
Spotted Deer	108	74.5	66	84.6	78.0
Wild Boar	16	11.0	2	2.6	8.1
Rhesus Macaque	8	5.5	1	1.3	4.0
Porcupine	2	1.4	0	0.0	0.9
Leopard Cat	1	0.7	0	0.0	0.5
Irrawaddy Dolphin (stranded carcase)	0	0.0	1	1.3	0.5
Lesser Adjutant	3	2.1	5	6.4	3.6
Red Junglefowl	1	0.7	1	1.3	0.9
Mud Crab	1	0.7	0	0.0	0.4
Water Monitor	0	0.0	2	2.5	0.9
Unidentified	5	3.4	0	0.0	2.2

Table 3: Estimated average number of collectable scats produced from individual prey animals and relative numbers of different prey species killed by Tigers in the Sundarbans East Wildlife Sanctuary

Prey species	Weight (kg)	Frequency of occurrence in scats	No. of collectable scats produced/ kill	Total no. of animals eaten to provide collected-scats	Relative no. of prey animals killed (%)
Spotted Deer	47.0[1]	108	13.1	8.2	29.9
Wild Boar	32.0[1]	16	10.3	1.6	5.8
Rhesus Macaque	4.0[1]	8	1.9	4.2	15.3
Porcupine	8.0[2]	2	3.5	0.6	2.2
Leopard Cat	3.0[3]	1	1.4	0.7	2.6
Lesser Adjutant	4.0[4]	3	1.9	1.6	5.8
Red Junglefowl	0.6[5]	1	0.3	3.3	12.1
Mud Crab	0.3[6]	1	0.2	5.0	18.3
Unidentified	5.0[7]	5	2.3	2.2	8.0

N.B. Mainly the minimum adult weights of the prey species were considered.
[1]Source: Karanth & Sunquist (1992); [2]Source: Karanth & Sunquist (1995); [3]Source: Prater (1971); [4]Source: www.ndngrd.com; [5]Source: www.international.tamu.edu; [6]Source: local crab collectors; [7]Source: arbitrarily assumed, as in Karanth & Sunquist (1995)

of a large amount of soil proves that these were not accidentally ingested.

Prey abundance versus prey selection

The selectivity index (S) for six potential prey species shows that Wild Boar and Lesser Adjutant were high ranked; Spotted Deer, Rhesus Macaque and Red Junglefowl were middle ranked; and Water Monitor was a non-used species (Table 4). It is notable that the two least-available prey species were highest in the ranking, i.e., rates of their selectivity by Tigers were highest in comparison to their abundance.

Age and health of kills

The mean lengths of lower jaw bone and diastema of the Spotted Deer were 18.7 cm (n = 34, range = 12.0-21.7 cm, sd = 2.1) and 5.0 cm (n = 34, range = 3.2-6.3 cm, sd = 0.8), respectively. Other than the Spotted Deer, only two intact lower jaws of Wild Boar were found. The lower jaw lengths of these two specimens were 20.5 and 21.7 cm, and the diastema length in both cases was 0.5 cm. Most of the kills were adult animals (based on fresh kills – 56.5%, based on eruption of teeth – 76.5%) (Table 5), and were in good condition before they were killed (78.8%) (Table 6).

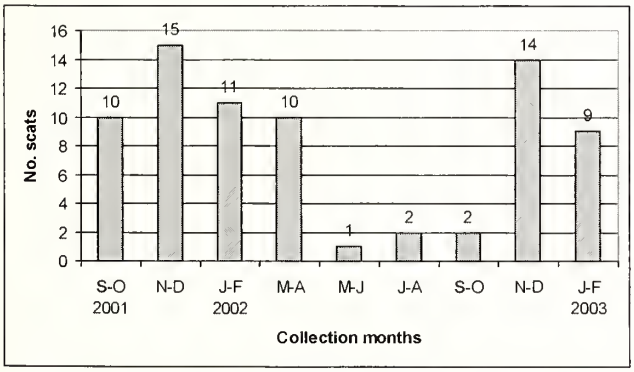

Fig. 4: Bi-monthly occurrence of Tiger scats with soil consisting of more than 50% of the volume in the Sundarbans East Wildlife Sanctuary

Abundance and selection of Spotted Deer in different age classes

Based on Ivlev's selectivity index, the values of D for adult, yearling and fawn age classes of the Spotted Deer were calculated at 0.112, -0.094 and -0.113, respectively. Since the value is positive only for adult age class and negative for yearling and fawn classes, it can be concluded that the adult Spotted Deer were positively selected, whereas the yearling and fawn Spotted Deer were negatively selected. In other words, the predation was higher than the abundance of adults, but lower than the abundance of yearling and fawn.

DISCUSSION

Prey selection

The preference for large prey species (Spotted Deer), as found in this study, supports the hypotheses related to foraging theory (Stephens and Krebs 1987), which suggest

Table 4: Prey species ranking based on selectivity index

Prey species	Selectivity index (S)	Rank of the prey species
Spotted Deer	-0.05	Middle
Wild Boar	0.77	High
Rhesus Macaque	0.19	Middle
Lesser Adjutant	0.72	High
Red Junglefowl	0.04	Middle
Water Monitor	-1.00	Non-used

that predators may select species containing the most 'profitable' prey, as measured by the ratio of energy gain to handling time (MacArthur and Pianka 1966; Schoener 1971; Charnov 1976; Scheel 1993; Karanth and Sunquist 1995). For large felids the most profitable prey type would seem to be the largest available prey that could be safely killed, but the importance of search time, encounter rates, and the energetic costs of capture for various prey types also need to be considered (Sunquist and Sunquist 1989). Tiger and Leopard *Panthera pardus* usually catch the kill when it is large enough to afford more than one meal (Johnsingh 1983).

It has been reported that Tigers prefer to hunt larger prey species (>176 kg), especially when there are other carnivores like Leopards and Asiatic Wild Dogs *Cuon alpinus* in the same habitat (Schaller 1972; Karanth and Sunquist 1995, 2000; Bagchi *et al.* 2003). In the Sundarbans, Tigers mainly hunt the largest available prey species, i.e., the Spotted Deer, despite the fact that there is no Leopard over there.

Reza *et al.* (2001) reported that in the Sundarbans East WS the average percentage by weight of Spotted Deer, Wild Boar and Rhesus Macaque hair, and unidentified animal parts and soluble material were 69, 15, 5, 4 and 6, respectively. Their methods were questionable, because the weight, size and density of hairs of these three species were not uniform. Hence, the relative weights of hair samples in scats do not accurately represent either relative biomass or relative numbers of different prey species consumed. They have found the mean weight of scat as 122 gm and the Spotted Deer as the principal prey, which was generally the same as in this study.

According to Tamang (1993), the principal prey of the Tiger in the Sundarbans are Spotted Deer and Wild Boar, but Tigers are opportunist feeders and there are records of predation of Rhesus Macaque, Barking Deer *Muntiacus muntjak*, otters, small carnivores, birds (mainly Red Junglefowl), lizards (*Varanus* spp.), other reptiles, frogs, fish, crabs, and occasionally humans. My findings generally agree with this.

In India, the Spotted Deer is the main prey of the tiger in Kanha, Bandipur and Nagarhole (Schaller 1967; Johnsingh 1983; Karanth and Sunquist 1995), but it is the second or third main prey in Ranthambhore, Panna and Melghat (Koppikar and Sabnis 1979; Gogate and Chundawat 1997; Bagchi *et al.* 2003). In Huai Kha Kheng, Thailand, the Barking Deer is the main prey species (Rabinowitz 1989). In the Russian Far East, Elk *Cervus elaphus* and Wild Boar were consistently the two key components of the Tiger diet (Abramov 1962; Miquelle *et al.* 1996). Karanth and Sunquist (1995) reported that in Nagarhole, India, the biomass of the Spotted Deer, Sambar, Gaur *Bos frontalis*, Wild Boar, Barking Deer and Common Langur *Semnopithecus entellus* comprised 97.6% of the biomass killed by Tigers. In contrast, I have found that the Spotted Deer alone was 80.1% of the biomass consumed by Tigers in the Sundarbans.

Non-food items in scats

Other than typical food items, soil and sungrass blades have been reported in Tiger scat samples (Powell 1957; Schaller 1967; Johnsingh 1983; Reza *et al.* 2001). During this study, soil was found in large quantities (more than 50% of the volume) in 51% of the scat samples, which is the highest proportion of soil-containing scats ever reported. Schaller (1967) reported that scats with soil and grass (more than 50% of the volume) represented 3.8% and 2.3% of all types of items eaten by Tigers in Kanha, India. He found most of the soil-containing scats during October-December, i.e., early winter, and suggested a seasonal incidence of soil-eating. A similar trend was found in this study, in which more than 80% of the soil-containing (more than 50% of the volume) scats were found in winter (October-March), with the peak in November-December (*c.* 15%). In Bandipur, India, Johnsingh (1983) found that out of 36 scats, three contained soil and two contained grass (more than 50% of the volume). Reza *et al.* (2001) mentioned the occurrence of an average 6% weight of scats composed of soil in the Sundarbans, but in this study, soil was found to constitute more than half of the volume of 51% of scat samples. This means that the percentage of weight of soil was definitely much higher than 6%. Other than soil, I have found significant amount of sungrass blades in one scat. The ingestion of soil and sungrass blades by Tigers is probably to meet mineral requirements, for better digestion and/or to scour the digestive system for internal parasites. In Kanha, India, one grass-blade-rich Tiger scat had a tapeworm (Schaller 1967).

Table 5: Age of Spotted Deer kills based on observation of kills and on the eruption of teeth in the lower jaw

Age based on kills			Age based on eruption of teeth		
Class	No.	%	Class	No.	%
Adult	26	56.5	Adult	26	76.5
Yearling	11	23.9	Yearling	6	17.6
Fawn	9	19.6	Fawn	2	5.9

Table 6: Condition of Spotted Deer kills

Condition		
Class	No.	%
Good	52	78.8
Moderate	14	21.2
Bad	0	0

Prey abundance versus prey selection

In Nagarhole, India, Karanth and Sunquist (1995) studied prey selection by Tiger, Leopard and Asiatic Wild Dog. They concluded that all three predators selected prey species non-randomly, which was mainly based on the prey size and encounter probability. In the Sundarbans, I have also found that Tigers non-randomly selected the prey species and the largest and commonest available ungulate (Spotted Deer) forms the bulk of the diet.

In Bandipur, India, Tiger scat and kill data reveal that proportionately fewer Spotted Deer were killed than were present in the population (Johnsingh 1983, 1993). This can be attributed to the anti-predator behaviour of the Spotted Deer, which assemble in open areas to spend the night, where they are relatively less vulnerable to Tiger predation. The Spotted Deer was virtually the only large prey in the Sundarbans, so it is difficult to compare my conclusions with those of Johnsingh (1983, 1993). In general, prey size together with the abundance is the most important factor driving the prey consumption. However, there are many other factors that might be involved in Tiger predation, such as anti-predator behaviour, detectability, and 'profitability' in terms of energy gain.

Based on prey selectivity in comparison to abundance, the index of selectivity of the six potential prey species in the Sundarbans East WS identified Wild Boar and Lesser Adjutant as the two highest-ranking species. These two species, however, contribute little in biomass abundance and biomass consumed by Tigers in the Sundarbans, so highest-ranking species should not be confused with commonly-preyed species. Since both Wild Boar and Lesser Adjutant are largely solitary, they are more vulnerable to Tiger predation. According to van Orsdol (1981), Lion *Panthera leo* hunting success varied with the size of prey group; single and paired prey were more easily caught than those in larger groups. Moreover, Tigers probably preferred Wild Boar and Lesser Adjutant as a change in common prey item (Spotted Deer). Although the Water Monitor was common, it has been identified as a non-used species (there was no trace of it in scats) probably because of its smaller size and aquatic habitation, and like most mammalian species, Tigers might be reluctant to hunt such a reptile.

Selectivity for age classes

Predators may preferentially select substandard (juveniles and young) animals, because they are less adapted to escape (Hornocker 1970; Mech 1970; Schaller 1972; Curio 1976; Vitale 1989). Karanth and Sunquist (1995), and Miquelle *et al.* (1996) reported that although Tigers predominantly kill adult prey, the young or substandard prey is killed in relatively high proportions.

In my study most of the Tiger kills were adult animals, which do not agree with the above-mentioned findings. There was no tendency to prefer young or substandard prey, probably because it may not be 'profitable' to hunt young Spotted Deer instead of the adult because of size. The adult Spotted Deer is not too big to pose any challenge to the Tiger and in the Sundarbans there is enough cover for the Tiger to ambush. My findings from Tiger kills and their jaws, however, could be adult-biased, because young and juvenile animals are smaller and they are more commonly eaten completely by predators (Schaller 1967; Sunquist 1981; Johnsingh *et al.* 1991). Moreover, the kill detectability by the researcher is normally large-animal-biased (Ruggiero 1991).

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REFERENCES

Abramov, V.K. (1962): On the biology of the Amur Tiger, *Panthera tigris longipilis*, Fitzinger, 1868. *Acta Societatis Zoologicae Bohemoslovenicae 26*: 189-202.

Ackerman, B.B., F.G. Lindzey & T.P. Hemker (1984): Cougar food habits in southern Utah. *Journal of Wildlife Management 48*: 147-155.

Amerasinghe, F.P. (1983): The structure and identification of the hair of the mammals of Sri Lanka. *Ceylon Journal of Science (Biological Science) 16*: 76-125.

Ashby, K.R. & C. Santiapillai (1986): The life expectancy of wild artiodactyle herbivores, Water Buffalo (*Bubalus bubalis*), Sambar (*Cervus unicolor*), Spotted Deer (*Axis axis*), and Wild Pig (*Sus scrofa*), in Ruhuna National Park, Sri Lanka, and the consequences for management. *Tigerpaper 13(2)*: 1-7.

Bagchi, S., S.P. Goyal & K. Sankar (2003): Prey abundance and prey selection by Tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. *Journal of Zoology 260(3)*: 285-290.

Ballard, W.B., G.M. Matson & P.R. Krausman (1995): Comparison of two methods to age gray wolf teeth. Occasional publication no. 35. Pp. 455-460. *In*: Carbyn, L.N., S.H. Fritts & D.R. Seip (Eds): Ecology and Conservation of Wolves in a Changing World. Canadian Circumpolar Institute, Canada.

Berger, J., B. Stacey-Peter, L. Bellis & M.P. Johnson (2001): A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian Neotropical migrants. *Ecological Applications 11*: 947-960.

Charnov, E.L. (1976): Optimal foraging: the marginal value theorem.

Theoretical Population Biology 9: 129-136.

Clutton-Brock, T.H. & P.H. Harvey (1983): The functional significance of variation in body size among mammals. Special publication no. 7. Pp. 632-658. *In*: Eisenberg, J.F. & D.G. Kleiman (Eds): Advances in the Study of Mammalian Behaviour. American Society of Mammalogists, Kansas, USA.

Curio, E. (1976): Ethology of Predation. Springer-Verlag, Berlin, Germany.

Emmons, L.H. (1987): Comparative feeding ecology of felids in a Neotropical rainforest. *Behavioural Ecology and Sociobiology 20*: 271-283.

Floyd, T.J., L.D. Mech & P.J. Jordan (1978): Relating wolf scat contents to prey consumed. *Journal of Wildlife Management 42*: 528-532.

Gogate, N. & R.S. Chundawat (1997): Ecology of Tiger: to enable a realistic projection of the requirements needed to maintain a demographically viable population of tigers in India. Second Progress Report to – Save The Tiger Fund, Washington, DC, USA.

Hornocker, M.G. (1970): An analysis of Mountain Lion predation upon Mule Deer and Elk in the Idaho Primitive Area. *Wildlife Monograph 21*: 1-29.

Johnsingh, A.J.T. (1983): Large mammalian prey-predators in Bandipur. *J. Bombay Nat. Hist. Soc. 80*: 1-57.

Johnsingh, A.J.T. (1993) Prey selection in three large sympatric carnivores in Bandipur. *Mammalia 56(4)*: 517-526.

Johnsingh, A.J.T., H.S. Panwar & W.A. Rodgers (1991): Ecology and conservation of large felids in India. Pp. 160-166. *In*: Proceedings of the International Symposium on Wildlife Conservation, 21-25 August 1990. Tsukuba and Yokohama, Japan.

Julliot, C. (1996): Fruit choice by Red Howler Monkeys (*Alouatta seniculus*) in a tropical rain forest. *American Journal of Primatology 40*: 261-282.

Karanth, K.U. & M.E. Sunquist (1992): Population structure, density and biomass of large herbivores in the tropical forests of Nagarhole, India. *Journal of Tropical Ecology 8*: 21-35.

Karanth, K.U. & M.E. Sunquist (1995): Prey selection by Tiger, Leopard and Dhole in tropical forests. *Journal of Animal Ecology 64*: 439-450.

Karanth, K.U. & M.E. Sunquist (2000): Behavioural correlates of predation by Tiger (*Panthera tigris*), Leopard (*Panthera pardus*) and Dhole (*Cuon alpinus*) in Nagarhole, India. *Journal of Zoology London 250*: 255-265.

Khan, M.M.H. (2004): Ecology and conservation of the Bengal Tiger in the Sundarbans mangrove forest of Bangladesh. Ph.D. dissertation. University of Cambridge, Cambridge, UK. 297 pp.

Khorozyan, I. & A. Malkhasyan (2002): Ecology of the Leopard (*Panthera pardus*) in Khosrov Reserve, Armenia: implications for conservation. Societa Zoologica 'La Torbiera', Italy. Scientific report 6: 1-41.

Kitsos, A.J., M.J. Hunter, J.H. Sabnis & A. Mehta (1995): A guide to the identification of some Indian mammal hairs. Pp. 125-130. *In*: Berwick, S.H. & V.B. Saharia (Eds): The Development of International Principles and Practices of Wildlife Research and Management, Asian and American Approaches. Oxford University Press, New Delhi, India.

Koppikar, B.R. & J.H. Sabnis (1976): Identification of hairs of some Indian mammals. *J. Bombay Nat. Hist. Soc. 73*: 5-20, *74*: 50-59.

Koppikar, B.R. & J.H. Sabnis (1979): Faecal hair remains serve as evidence for determination of food habit of Tiger. Paper presented at International Symposium on Tiger (ISOT), New Delhi, India. 10 pp.

Korschgen, L.J. (1971): Procedures for food-habits analysis. Pp. 233-258. *In*: Giles, R.H. (Ed.): Wildlife Management Technique, 3rd edn. The Wildlife Society, London, UK.

Landon, D.B., C.A. Waite, R.O. Peterson & L.D. Mech (1998): Evaluation of age determination techniques for gray wolves. *Journal of Wildlife Management 62*: 674-682.

MacArthur, R.H. & E.R. Pianka (1966): On the optimal use of a patchy environment. *American Naturalist 100*: 603-609.

Mech, L.D. (1970): The Wolf: ecology and behaviour of an endangered species. The Natural History Press, New York, USA. 428 pp.

Miquelle, D.G., E.N. Smirnov, H.B. Quigley, M.G. Hornocker, I.G. Nikolaev & E.N. Matyushkin (1996): Food habits of Amur Tigers in Sikhote-Alin Zapovednik and the Russian Far East, and implications for conservation. *Journal of Wildlife Research 1(2)*: 138-147.

Mukherjee, S., S.P. Goyal & R. Chellam (1994): Standardisation of scat analysis technique for Leopards (*Panthera pardus*) in Gir National Park, Western India. *Mammalia 58*: 139-143.

Okarma, H., W. Jedrzejewski, K. Schmidt, R. Kowalczyk & B. Jedrzejewska (1997): Predation of Eurasian Lynx on Roe Deer and Red Deer in Bialowieza Primeval Forest, Poland. *Acta Theriologica 42*: 203-224.

Panwar, H.S. (1990): Tiger's food in Kanha National Park. *WII Newsletter 5(1)*: 12-15.

Powell, A. (1957): Call of the Tiger. London, UK. 199 pp.

Prater, S.H. (1971): The Book of Indian Animals. Bombay Natural History Society and Oxford University Press, Bombay, India. 324 pp.

Putman, R.J. (1984): Facts from faeces. *Mammal Review 14*: 79-97.

Rabinowitz, A.R. (1989): The density and behaviour of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Natural History Bulletin of the Siam Society 37(2)*: 235-251.

Ramakrishnan, U., R.G. Coss & N.W. Pelkey (1999): Tiger decline caused by the reduction of large ungulate prey: evidence from a study of Leopard diets in southern India. *Biological Conservation 89(2)*: 113-120.

Reynolds, J.C. & N.J. Aebischer (1991): Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. *Mammal Review 21*: 97-122.

Reza, A.H.M.A., M.M. Feeroz & M.A. Islam (2001): Food habits of the Bengal Tiger (*Panthera tigris tigris*) in the Sundarbans. *Bangladesh Journal of Zoology 29(2)*: 173-179.

Riney, T. (1982): Study and Management of Large Mammals. John Wiley & Sons Ltd, New York, USA.

Ruggiero, R.G. (1991): Prey selection of the Lion (*Panthera leo* L.) in the Manavo-Gounda-St Floris National Park, Central African Republic. *Mammalia 55*: 24-33.

Schaller, G.B. (1967): The Deer and the Tiger. University of Chicago Press, Chicago, USA. 370 pp.

Schaller, G.B. (1972): The Serengeti Lion: a study of predator-prey relations. University of Chicago Press, Chicago, USA. 504 pp.

Scheel, D. (1993): Profitability, encounter rates, and prey choice of African Lions. *Behavioural Ecology 4*: 90-97.

Schoener, T.W. (1971): Theory of feeding strategies. *Annual Review of the Ecological System 2*: 369-404.

Sinclair, A.R.E. & P. Duncan (1972): Indices of conditions in tropical ruminants. *East African Wildlife Journal 10*: 143-149.

Smuts, G.L. (1978): Interrelations between predators, prey, and their environment. *BioScience 28(5)*: 316-320.

Sourd, C. (1983): Etude des modes d'exploitation des resources fruitieres par *Cercopithecus cephus* au cours d'un cycle annuel (in French). [Study of exploitation of food resources for *Cercopithecus cephus*] Third cycle thesis, University of Rennes, Rennes.

Stephens, D.W. & J.R. Krebs (1987): Foraging Theory. Princeton University Press, Princeton. 262 pp.

Sunquist, M.E. (1981): Social organization of Tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. Smithsonian Contribution to Zoology *336*: 1-98.

Sunquist, M.E., K.U. Karanth & F.C. Sunquist (1999): Ecology, behaviour and resilience of the Tiger and its conservation needs. Pp. 5-18. *In*: Seidensticker, J., S. Christie & P. Jackson (Eds): Riding the Tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK.

Sunquist, M.E. & F.C. Sunquist (1989): Ecological constraints on predation by large felids. Pp. 283-301. *In*: Gittleman, J.L. (Ed.): Carnivore Behaviour, Ecology and Evolution, Cornell University Press, Ithaca.

Tamang, K.M. (1993): Wildlife management plan for the Sundarbans reserved forest. Report of the FAO/UNDP project (no. BGD/84/056), Dhaka, Bangladesh. 113 pp.

Terborgh, J. (1999): Requiem for Nature. Island Press, Washington, DC, USA. 246 pp.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabudin, G. Orihuela, M. Riveros, R. Ascanio, G.H. Adler, T.D. Lambert & L. Balbas (2002): Ecological meltdown in predator-free forest fragments. *Science 294*: 1,923.

van Lavieren, L.P. (1983): Wildlife management in the Tropics with special emphasis on South East Asia (report), part 2. School of Environmental Conservation Management, Bogor. 75 pp.

van Orsdol, K.G. (1981): Lion predation in Rwenzori National Park, Uganda. Ph.D. dissertation. University of Cambridge, Cambridge, UK.

Vitale, A.F. (1989): Changes in the anti-predator responses of wild rabbits, *Oryctolagus cuniculus* (L.) with age and experience. *Behaviour 110*: 47-61.

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